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THE USTILAGINEÆ, OR SMUTS, OF CONNECTICUT

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The Ustilagineæ, or Smuts, of Connecticut.

GENERAL CHARACTERS OF THE SMUTS.

The Ustilagineæ are an order of parasitic fungi commonly known as the smuts, of which corn, oat, and onion smuts are familiar examples. See Figs. 55, 43, 42. Thus the more evident characters of these fungi are the black, dusty masses that break out on the surface of the infected plants (hosts). In these macroscopic characters the smuts are often very similar to the rusts, but with a little experience one can readily distinguish them from these even with the naked eye. The dusty *uredo* stage of the rusts, for instance, is of a lighter reddish color, and the darker *teleuto* stage is usually more firmly embedded in the plant tissues, than are the smuts. Not all of the smuts, however, produce dark dusty outbreaks, since the white smuts are light colored and usually permanently embedded in the tissues of the host. Generally they occur in the leaves, and often are distinguished by light colored spots produced without distortion of tissues. More experience is needed to distinguish these forms. See Figs. 29-34.

The smuts occur on a great variety of flowering plants, and at least 35 different families of plants in North America and 17 in Connecticut are subject to their attack. The grasses, however, are by far the most frequent hosts. Between 500 and 600 species of smuts have been described from different parts of the world, and over 200 of these occur in North America. The number of species known from this state * is 50, and these represent 12 of the 19 genera reported from North America. While time no doubt will reveal a few more species and a greater number of hosts not reported here, we may still consider the group rather thoroughly worked up, since, as yet, only one other state has reported a greater number of species.

* The list of smuts reported in this paper is based chiefly on the collections made by the writer during the past three seasons. Specimens of these are to be found in the herbarium of the Conn. Agr. Exp. Station at New Haven and in the writer's herbarium. Collections made by others are indicated in each case by the name of the collector.

LIFE HISTORY OF THE SMUTS.

In the study of these fungi, there are three parts that we need to consider, namely, the *mycelium,* the *spores,* and the *sori.*

Mycelium is the technical name for the vegetative part of the smut, by means of which it spreads through its host and gathers nourishment. This consists of microscopic threads confined to the interior of the host, so it is necessary to examine very thin cross sections of the tissues under the microscope to see this stage. See Fig. 26. These threads vary but little with the different species, and therefore are of no value in classifying the different species. They are simple, hyaline, more or less branched, and at first filled with protoplasmic contents, but gradually lose most of their contents and become septate. They push their way between the cells of the host or sometimes through them. Usually, however, they enter the cells only by short special branches called *haustoria,* whose special function is to gather nourishment from the cell. The mycelium may be localized or rather generally spread through the host. In those cases where it gains entrance through the germinating seed, it usually remains evident finally only at the nodes or where it breaks forth to the exterior in its fruiting stage. In perennial plants the mycelium often becomes established in the perennial parts, from which each year it sends threads into the new growth.

Eventually the mycelium becomes prominent in certain regions of the host, and there undergoes special modification to give rise to the reproductive or spore stage. The walls of the mycelial threads that form the spores are generally indistinct through more or less complete gelatinization. The spores are usually formed from contents in the interior of these fertile threads. This gelatinization apparently serves to nourish the developing spores, as often all signs of the threads disappear on maturity of the spores. In some cases, as in the genus *Neovossia,* Fig. 13, and often in *Entyloma,* however, these threads remain as more or less evident envelopes to the spores.

Spores are the bodies by which the smuts reproduce themselves. See Figs. 1-20. They are the evident, usually ex-

ternal part of the fungus, making up the smutty masses visible to the naked eye, and are the characteristic and variable parts upon which species are based. The spores are usually so formed that at maturity they break out to the exterior of the host in a dusty mass that is easily scattered, thus securing their dispersal. In some species, however, they are embedded in the host so that they are liberated only on the rotting of the tissues, and sometimes they germinate *in situ,* and secure their dispersal by the formation of secondary spores of a different nature. While easily seen in mass, the spores are really microscopic in size, varying according to species from 4μ to 35μ.* They are usually subspherical or spherical, but vary to ovoid, ellipsoidal, or even oblong. Pressure often makes them more or less polyhedral, or irregularly so. They are generally simple, consisting of single separate cells; but are sometimes bound more or less permanently into spore balls, Figs. 7*a,* 10*a.* These spore balls may consist entirely of fertile cells (spores) or they may have an external coating (cortex) of sterile cells, Fig. 19, or an internal matrix of sterile cells or even of threads, Fig. 20. The spore walls may be smooth, or marked with minute spines (echinulations if sharp, verruculations if dull), or reticulated with a net-work of ridges or wings. In color they are hyaline, yellowish, reddish or olive brown, violet, or purplish. Often the color is so deep that the spores are opaque or nearly so. Upon these variations the genera and species are chiefly classified, though on the whole the variations are not so great as with many of the other fungi. This is partly due to the fact that the spore-producing threads are not diversified or permanent.

In some few species, most frequently in the genus *Entyloma,* the mycelium also gives rise to secondary spores called *conidia.* These are usually hyaline, elongated, ephemeral, and are produced originally on the exterior of the host, generally from mycelial tufts protruding through the stomates and forming these conidia at their tips. Their object is to spread the smut over the host or to new hosts immediately.

Sori are the evident masses of the spores that break out singly or in clusters on the various parts of the hosts. See

* A μ, or micron, is one twenty-five thousandth of an inch.

Figs. 27-55. These are protected more or less permanently by thin coverings of plant tissue, or in some genera, as *Sphacelotheca,* and often in *Cintractia,* by false membranes composed chiefly of fungous cells or threads, Fig. 5*a*. The sori vary greatly in size, sometimes forming outbreaks smaller than a pin-head, and sometimes, as often in corn smut, reaching several inches in diameter. Usually each species has a definite place on its host where the sori appear. This may be on the leaves, Fig. 35, on the stems, Fig. 28, in the blossoms as a whole, Fig. 54, or confined to the anthers, ovaries, Fig. 52, or seeds, Fig. 48. Occasionally a smut may break out in any of these places. In the grasses, when infecting the inflorescence, the sorus may be confined to the ovary, infest the spikelet as a whole, or even involve the entire inflorescence. Sometimes all of the ovaries or spikelets are infested and sometimes only part of them. The characters of the sori, of course, are modified somewhat by the part of the host in which they develop, and also by the kind of host on which the smut occurs. Usually the sori are dusty and easily dissipated. With a few species they are hard, and the agglutinated spore mass is disseminated by gradual disintegration, often through the absorption and loss of water. In these cases there is sometimes a gradual ripening of the spores from the outside of the sorus inward. With some genera (*Entyloma, Doassansia,* etc.) the sorus is rather permanently embedded in the tissues of the host, usually in the leaves, and often produces only a discoloration of these. The species of one of the European genera form gall-like growths in the roots.

Germination of Spores. There are two chief types of germination of the Ustilagineæ upon which the two families are based. In the *Ustilaginaceæ,* Fig. 21, the spores, when placed in a drop of water, send out a single, hyaline thread, several times their length, which usually divides into about four cells by cross partitions, or septa. This is called the *promycelium.* Usually at the apex of each cell one or more elongated thin-walled spores, or *sporidia,* are budded out, the apical cell bearing its sporidium terminally and the others laterally. The sporidia when full-sized are pinched off at the base, and others are sent out until the protoplasm of the cell

is exhausted. These sporidia germinate by a short slender thread (infection thread) that usually pushes out from near one end, Fig. 24. In some species the cells of the promycelium, instead of forming the sporidia, give rise directly to the infection threads, Fig. 23. Sometimes the adjacent cells of the promycelium become connected by closely applied short threads, forming buckle or knee joints, and from these may develop infection threads. Some species germinate directly into elongated threads which scarcely partake of the nature of a promycelium. When nutrient is added to the drop of water, the spores germinate much more luxuriantly, the sporidia usually sprouting out other sporidia while still attached to the promycelium. Especially in a solid cultural medium these chains develop a more or less complicated system of branching, Fig. 25. In a liquid solution, the sporidia usually soon fall off from the promycelium, but continue to multiply by the yeast fashions of budding new sporidia, which soon separate and develop others, until the nourishment is exhausted. Then the sporidia may develop infection threads.

The second chief type of germination is shown by the species of *Tilletiaceæ,* Fig. 22. The simple or septate promycelium in this case bears all of the elongated sporidia in a terminal cluster. Sometimes these primary sporidia develop terminal secondary sporidia. With some species the sporidia, before or after falling off from the promycelium, become yoked in pairs by short connecting threads. In nutrient solutions some of the species develop finally a complicated mycelium that bears numerous aërial sporidia or conidia quite different from the normal type produced in water. The conidia develop infection threads on germination.

Infection of Host. The host is entered by the fine infection threads of the promycelia or the sporidia boring through its tissues into the interior. Once inside, these develop the mycelium of which we have already spoken. Many of the smuts infect their host only through the young hypocotyl or epicotyl of the seedling. In these cases the smut usually can not gain successful entrance after the plants appear above ground. Once inside, the mycelium rapidly penetrates the young tissues, seeking to gain access to the growing tip, where

it then follows the upward growth of the plant, often not giving evidence of its presence until it breaks out in its spore stage in the fruiting organs of the host two or three months later. This is the case with the oat smuts, wheat and barley smuts, and the grain smut of broom-corn. In this latter case the mycelium has traveled upward through six to ten feet of the cane. In other species infection may take place through any very young tissue of the host upon which the germs may be blown or washed into contact. This is the case with corn, and the corn smut appears soon after infection in its smutty outbreaks, the mycelium usually remaining localized. With the *Entylomas* the infection is largely confined to the leaves, and apparently the mycelium is limited to the vicinity of the sorus.

ECONOMIC IMPORTANCE.

Injury. While most of the smuts occur on plants of no economic importance, there are at least twenty-five species in America that do more or less injury to cultivated plants. Some of these cause such serious injury that they are counted among the worst species of parasitic fungi. It is with the cereals that the smuts do most damage. Wheat, oats, barley, rye, and corn are all subject to attacks from one or more species. With the first three hosts the smuts break out in the inflorescence, entirely preventing the formation of the seed. It thus becomes an easy matter to determine rather accurately the per cent. of loss in fields of these grains by counting the number of smutted and of free heads in a given area. Oat smut, for instance, in our central states generally claims from one to fifteen per cent. of the grain, and in some few fields as high as thirty or forty per cent. has been destroyed. In Illinois there is perhaps an average loss per year of one million dollars worth of oats, caused by the two smuts of this plant. In Indiana Arthur found one field of wheat where fifty per cent. of the grain was destroyed by the stinking smut. In the northwestern states, in the wheat districts, the loss caused by this latter smut is very great, as it is one of their worst fungous pests. When abundant it renders the grain inferior for milling purposes, as the spores may be so numerous in the flour that they darken

it. In South Carolina during recent years a smut of rice has been introduced from Japan, and causes some loss to this crop. In the eastern states where onions are raised extensively, the onion smut often does considerable injury. In this case the smut becomes established in the soil and often prevents profitable onion culture on this land. Corn smut is common everywhere, and especially on sweet corn causes considerable injury. In Connecticut the most injurious smuts, from an economic standpoint, are those of onion, corn, barley, and oats.

Prevention. With those plants where infection takes place through the germinating seed, the danger usually comes from the spores that mechanically adhere to the seed. It has been found that, if these are killed, the crop from this seed will be free from smut. Investigations have shown that certain treatment of the grain with chemical solutions or with hot water will kill the spores with little or no injury to the seed. For instance, it has long been known that soaking the seed of wheat in a solution of copper sulphate of a certain strength for a certain time serves to prevent or lessen the amount of stinking smut in the crop. Later it was found that soaking the seed for ten or fifteen minutes in hot water at a temperature of 132° to 135° F. was a more efficient remedy, since there was less likelihood of injury to the seed. More recently still came the less cumbersome practice of sprinkling piles of the grain with formalin, one pint to fifty gallons of water, stirring the grain to thoroughly wet it, and leaving it in piles or in bags over night for the fumes to act on the spores. The smuts of oats, the covered smut of barley, the stinking smut of wheat, the grain smut of sorghum and broom-corn, and the grain smut of millet, have all yielded to seed treatment. The loose smuts of wheat and barley can be prevented or lessened by a severer method of the hot water treatment (in which a preliminary soaking of several hours in cold water precedes the hot water treatment), but this also injures the seed more or less, so that a greater quantity per acre must be sown. Corn smut can not be prevented by seed treatment, as the smut gains entrance through any young tissue of the host. Some experimenters have advocated the removal of the smut-balls as soon as they appear. It is known that the fungus develops aërial conidia

in manure, and so fresh manure applied to corn land is apt to increase the amount of smut. With onion smut we have a case where the seedlings while coming through the soil are infected by the smut established there through a previous smutted crop. Onions raised from sets in this land are little infected. Some success has been had in preventing this smut by treating the soil with a mixture of lime and sulphur, drilled into it at time of seeding.

SYSTEMATIC TREATMENT OF CONNECTICUT SPECIES.

The order *Ustilaginea* is divided into two families, based chiefly on the method of spore germination. They are the *Ustilaginaceæ* (represented in this state by the genera *Cintractia, Schizonella, Sorosporium, Sphacelotheca, Tolyposporium, Ustilago*), and the *Tilletiaceæ* (represented by *Doassansia, Entyloma, Neovossia, Tilletia, Tracya, Urocystis*).

Key to Genera.

I. Spores simple.
  A. Usually forming a dusty sorus at maturity (see also IB and IIIA1a).
    1. Large, usually 16-35μ.
      a. With an elongated hyaline appendage..... *Neovossia.*
      b. Without a conspicuous appendage. *Tilletia.*
    2. Small to medium, usually 5-18μ.
      a. Sorus covered with a false membrane of definite fungous cells.....*Sphacelotheca.*
      b. Protecting membrane of plant tissue only (sometimes with gelatinized hyphæ)..... *Ustilago.*
  B. More or less firmly agglutinated at maturity..... *Cintractia.*
  C. Permanently imbedded in leaves, producing discolored areas .....*Entyloma.*

II. Spores chiefly in pairs, forming an agglutinated sorus... *Schizonella.*

III. Spores in more or less permanent balls.
A. Forming a dusty or granular sorus at maturity.
1. Spore balls consisting only of spores.
a. Often evanescent (Ustilago-like spores)... *Sorosporium.*
b. Quite permanent, adhering by folds of spore coats ..... *Tolyposporium.*
2. Spore balls with a cortex of sterile cells..... *Urocystis.*
B. Permanently embedded in the plant tissues.
1. Spore balls with a definite cortex of sterile cells *Doassansia.*
2. Spore balls without cortex but with sterile threads in center ..... *Tracya.*

USTILAGINACEÆ Schröt.

The sori usually form exposed, dusty, or agglutinated spore masses. Germination is by means of a septate promycelium, which usually gives rise to terminal and lateral sporidia (capable of yeast-like multiplication in nutrient solutions), or else to infection threads. Figs. 21, 23-25.

Ustilago Rouss.

The sori occur on various parts of the host, according to the species, and at maturity form dusty, usually dark colored spore masses. The spores are single, separate, of small to medium size (5-18μ), and are produced irregularly in fertile threads that entirely disappear through gelatinization at maturity. Figs. 1-4, 43-55.

This is the most common and the typical genus of the smuts. Saccardo, in his *Sylloge Fungorum,* describes about 250 species for the world: 72 species occur in North America and 18 in Connecticut. A number of the species possess economic importance as parasites of the cereals.

Key to Species of Ustilago.

I. Spores olive or reddish brown.
A. Spores smooth.
1. Sori in leaves forming linear striæ..... *U. longissima.*

2. Sori in spikelets, ovoid.
   a. Spores usually lighter colored on one side, 5-9μ.
      * Spikelets entirely destroyed...*U. Hordei.*
      ** Spikelets smutted only at base..*U. levis.*
   b. Spores uniformly colored, 8-11μ..... *U. Crameri.*

B. Spores echinulate or verruculose.
1. Sorus in each spikelet, distinct.
   a. Spores usually lighter colored on one side, 5-9μ.
      * Host *Arrhenatherum avenaceum* (Oat Grass) .....*U. perennans.*
      ** Host *Avena sativa* (Oats)...*U. Avenæ.*
      *** Host *Hordeum vulgare* (Barley)..... *U. nuda.*
   b. Spores uniformly colored, 10-14μ..... *U. Panici-glauci.*
2. Sorus involving the entire panicle..... *U. Rabenhorstiana.*
3. Sori in the ovaries.
   a. Smooth and inconspicuous, 1-2 mm.
      * Spores echinulate .....*U. spermophora.*
      ** Spores verruculose .....*U. Eriocauli.*
   b. Hispid and conspicuous, 4-10 mm..... *U. sphærogena.*
4. Sori in leaves (rarely on stem).
   a. Forming nodular swellings, often at nodes *U. Crus-galli.*
   b. Forming linear striæ in the blades..... *U. striæformis.*
5. Sori breaking out on any part of host, often large .....*U. Zeæ.*

II. Spores golden brown, verrucose; sori in seeds..... *U. Oxalidis.*

III. Spores violet or purplish, reticulate, sori in flowers.
1. Reticulations rather fine, 1-3μ....*U. anomala.*
2. Reticulations rather coarse, 2-4μ.*U. utriculosa.*

Ustilago longissima (Sow.) Tul. Fig. 1. The sori form more or less distinct, linear striæ from a few mm. to length of leaf; the epidermal covering soon ruptures, and the dark reddish brown spore mass becomes scattered from the more or less shredded tissues. The spores are light brown, oblong, or more commonly ellipsoidal to spherical, smooth (or sometimes scarcely granular under an immersion lens), 4-8μ in length.

Host and Distr.: *Glyceria grandis,* Shaker Station, June 29, 1903.

This species undoubtedly has a wider distribution than indicated above.

Ustilago Hordei (Pers.) Kell. & Sw. Fig. 46. The sori occur in every spikelet, forming an ovate, adhering, purple-black spore mass, 6-10 mm. in length, and rather permanently covered by the thin, usually transparent plant tissue. The spores are reddish brown, slightly lighter colored on one side, chiefly subspherical or spherical, smooth, and 5-9μ, rarely (most elongated) 9-11μ, in length.

Host and Distr.: *Hordeum vulgare,* Whitneyville, Sept. 24, 1902.

This covered smut of barley is not nearly so common in this state as is the loose smut of the same host.

Ustilago levis (Kell. & Sw.) Magn. Fig. 45. The sori usually occur in all of the spikelets, are more or less hidden by the enveloping glumes (which may be infected only at their base or in the interior), and form rather permanent, black-brown, semi-agglutinated, ovate spore masses 6-10 mm. in length. The spores are reddish brown, slightly lighter colored on one side, chiefly subspherical or spherical, smooth, 5-9μ, rarely (most elongated) 11μ, in length.

Host and Distr.: *Avena sativa,* New Haven, July 10, July 28, 1902.

This hidden smut of oats is not so common in our oat fields as is the loose smut, *U. Avenæ.*

Ustilago Crameri Körn. Fig. 44. The sori occur in all of the spikelets of the spike, destroying especially the inner and basal parts, and form ovate dusty brown spore masses 2-4 mm. in length. The spores are reddish brown, ovoid to

subspherical, or occasionally more elongated or irregular, smooth, often with pitted contents, and 8-11μ in length.

Host and Distr.: *Setaria Italica,* New Haven, Sept. 11, 1903.

So far this species has been found in this state only once, in a small plot of Hungarian grass grown at the Experiment Station. In some of the central and western states it sometimes causes considerable injury to its host. It can be prevented by seed treatment with hot water, formalin, etc.

Ustilago perennans Rostr. The sori occupy all of the spikelets, usually destroying the basal and inner parts (sometimes even running down slightly on the pedicles); they are oblong, 3-8 mm. in length, and have a somewhat protected semi-dusty olive brown spore mass. The spores are chiefly subspherical or spherical, occasionally ellipsoidal to ovate, usually lighter colored on one side, minutely echinulate, especially on lighter side, and 5-8μ in length.

Host and Distr.: *Arrhenatherum avenaceum,* South Manchester (Thaxter).

This is closely related to the oat smuts. Its mycelium becomes perennial in the underground parts of the host, and so smuts the infested plants year after year.

Ustilago Avenæ (Pers.) Jens. Figs. 23, 43. The sori appear in all of the spikelets, completely destroying all the floral parts, except a very temporary transparent covering membrane; eventually the olive brown dusty spore mass becomes dissipated, leaving behind only the naked pedicles. The spores are reddish brown, lighter colored on one side, subspherical to spherical, or occasionally more elongated, minutely echinulate, especially on the lighter side, and chiefly 5-9μ in length.

Host and Distr.: *Avena sativa,* New Haven, July 8, July 28, Aug. 17, 1902, Aug. 9, 1903; West Cornwall, July 18, 1902; Westville, July 7, 1903; West Haven, July 22, 1903.

This is a common pest in the oat fields of the state, though the per cent. of infected plants is smaller than in the central and western states. It yields to seed treatment.

Ustilago nuda (Jens.) Kell. & Sw. Fig. 47. The sori infest all of the spikelets, changing each into an olive brown,

oblong, dusty spore mass about 6-10 mm. in length; this is very temporarily protected by a thin transparent membrane, and upon dispersal of the spores nothing remains but the naked rhachis. The spores are lighter colored on one side, subspherical to spherical, or occasionally more elongated, minutely echinulate, especially on the lighter side, and chiefly 5-9μ in length.

Host and Distr.: *Hordeum vulgare,* Storrs, 1901; New Haven, July 8, 1902, June 15, 1904; Whitneyville, Sept. 24, 1902; Westville, July 7, 1903.

This is the loose smut of barley, and is rather common in the fields of this crop. The smuts of barley, oats, and oat grass, as will be seen by the descriptions, are very similar, in fact were not long ago considered one species. It requires the modified form of the hot-water treatment to prevent the loose smut of barley.

Ustilago Panici-glauci (Wallr.) Wint. Fig. 49. The sori occur in all of the spikelets, are ovate, 2-3 mm. in length, and at first protected by thin transparent glumes, but soon rupture these, and scatter the dusty black-brown spore mass. The spores are dark reddish brown, ovoid, spherical or sometimes more elongated, prominently and abundantly echinulate, and 10-14μ in length.

Host and Distr.: *Setaria glauca,* Southington, Aug. 8, 1902; Bridgeport, Sept. 15, 1902; Berlin, Oct. 3, 1902; Glastonbury, Oct. 23, 1902; Andover, Sept. 15, 1903; New Canaan, Sept. 29, 1903; Manchester, Oct. 2, 1903.

Throughout the United States this is a common smut on the yellow fox-tail grass, though it does not occur on the green fox-tail.

Ustilago Rabenhorstiana Kühn. Fig. 50. The sorus involves the entire inflorescence, changing it into a linear or oblong body, 3-5 cm. in length, which is usually hidden by the enveloping leaf sheath; it is covered for a short time by a very fragile transparent plant membrane, and within the dusty brown-black spore mass are often elongated remains of the plant tissues. The spores are reddish or olive brown, ovoid to spherical, or occasionally slightly angled, echinulate to verruculose, and 10-14μ in length.

Host and Distr.: *Panicum sanguinale,* Centreville, Aug. 10, Sept. 1, 1902; Unionville, Aug. 26, 1902; New Haven, Sept., 1902, Oct. 5, 1904; Westville, Aug. 25, 1903; Montowese, Sept. 14, 1903; New Canaan, Sept. 29, 1903.

This is one of the common grass smuts here as elsewhere, and is to be looked for in the fall of the year.

Ustilago spermophora B. & C. Fig. 52. The brown-black dusty sori occur in the ovaries, infesting one here and there; they show as small ovate bodies, about 2 mm. in length, extending between the spreading glumes, and are at first protected by a thin ovary membrane at the apex of which are the remains of the styles. The spores are light brown, ovoid to subspherical, usually prominently echinulate, and 8-11μ, or occasionally 13μ in length.

Host and Distr.: *Eragrostis major,* New Haven, Oct. 31, 1902; Westville, Oct. 17, 1903.

The sori usually occur in only a few of the ovaries, and are so inconspicuous that the smut is easily overlooked. Fig. 52 shows isolated spikelets of the grass with a single sorus in each.

Ustilago Eriocauli (Mass.) Clint. The sori occur in the ovaries, scarcely showing between the glumes as slightly swollen ovoid bodies about 1 mm. in length; a thin membrane protects the rather firm, at first semi-agglutinated, but finally dusty, olive-black spore mass. The spores are polyhedral, subspherical, or occasionally more elongated, rather prominently verruculose, and 9-15μ in length.

Host and Distr.: *Eriocaulon septangulare,* Whitneyville, Sept. 21, 1902.

It requires very close examination to detect the flower heads containing this inconspicuous smut, since they resemble the normal ones. The smut should be searched for in the fall.

Ustilago sphærogena Burr. Fig. 53. The sori occupy the ovaries, forming ovate bodies, 4-10 mm. in length, which are covered by a tough hispid plant membrane that ruptures irregularly from the apex, disclosing at first an agglutinated, but finally a dusty, olive brown spore mass. The spores are ovoid to subspherical, prominently and sharply echinulate, and 9-12μ in length.

Host and Distr.: *Panicum Crus-galli,* Conn. (Setchell); Savin Rock, Sept. 14, 1902; Westville, Sept. 12, 1902.

This species and the next are very closely related, and occur on the same host, but are rarely, if ever, found together. Fig. 53 shows a portion of the flower panicle with a single unusually large sorus.

Ustilago Crus-galli Tr. & Earle. The sori form nodules often encircling the leaf node, or more rarely occur in place of inflorescence, infecting both leaves and stem; they are one to several cm. in diameter and protected by a tough hispid plant membrane, which on rupture discloses an olive brown spore mass. The spores are reddish brown, ovoid to spherical, occasionally more elongated, rather bluntly echinulate or even verruculose, and 10-14μ in length.

Host and Distr.: *Panicum Crus-galli,* New Haven, Sept. 11, 1903.

Only a single specimen of this smut was found on a cultivated variety of this barn-yard grass grown at the Experiment Station.

Ustilago striæformis (West.) Niessl. Fig. 51. The sori occur in the leaves, rarely in the inflorescence, forming short linear striæ, or by terminal fusion reaching several cm. in length, and laterally are often so crowded as to cover most of the leaf; at first they are covered by the epidermis, but this soon ruptures, and the dusty brown-black spore masses become scattered from the shredded tissues. The spores are reddish brown, vary from ellipsoidal to spherical, or occasionally irregular, are prominently echinulate, and 9-14μ in length.

Hosts and Distr.: *Agrostis alba* var. *vulgaris,* Whitneyville, July 20, 1902, May 9, 1903; Centreville, June 12, 1904; *Phleum pratense,* Whitneyville, May 9, 1903; New Haven, May 16, 1903.

Both of these hosts are economic plants grown for pasture or hay, but so far the smut has been found on them in this state only in door yards. Fig. 51 shows the leaves of *Agrostis alba* var. *vulgaris* shredded by this fungus.

Ustilago Zeæ (Beckm.) Ung. Figs. 2, 55. The sori break out on any part of the host, often forming prominent smut balls, though these vary from a few mm. to over a dcm.

in diameter, and also vary in shape according to the part attacked; the brownish black spore mass is at first covered with a whitish membrane, composed largely of semi-gelatinized fungous threads. The spores are ellipsoidal to spherical, occasionally irregular, prominently echinulate, and 8-11μ, rarely even 15μ, in length.

Hosts and Distr.: *Euchlæna luxurians,* New Haven, Sept. 11, 1903; *Zea Mays,* New Haven (Sturgis), Aug. 18, 1901 (Rorer); Southington, July 17, 1902; Westville, Aug. 14, Sept. 2, 1902, June 28, 1904; Hartford, Oct. 20, 1902; New Canaan, Sept. 29, 1903.

Corn smut is common on both the sweet and field varieties, though in this state the former is more subject to its attacks. Seed treatment will not prevent the smut, as it can gain entrance to its host through any exposed young tissue. The first host given is teosinte, a plant that is closely related to corn. Fig. 55 shows smutted staminate blossoms of corn reduced to one-half size.

Ustilago Oxalidis Ell. & Tr. Figs. 3, 48. The inconspicuous sori are found in the seeds, all or part of these being changed into reddish brown dusty spore masses, that show to the exterior only on the dehiscence of the otherwise little modified ovaries. The spores are golden yellow, ovoid to spherical, or rarely more elongated or irregular, coarsely verrucose, and 13-20μ in length.

Host and Distr.: *Oxalis stricta,* Yalesville, July, 1902; West Cornwall, July 18, 1902; New Haven, July, 1902; Whitneyville, Oct. 18, 1902, Sept. 9, 1903; Manchester, Oct. 2, 1903.

An inconspicuous conidial stage is also produced on the surface of the anthers of the infected flowers. These temporary spores are thin-walled and ovoid to subspherical. They are so placed that they are probably carried from the flowers by insects, as are pollen grains. Fig. 48 shows two ovaries in which all of the seeds have been changed into smutty bodies.

Ustilago anomala Kze. The sori occur in the essential organs of all the flowers, the floral envelopes forming a covering to the dusty, purplish spore mass. The spores are light violet, ovoid to spherical, occasionally somewhat irregular, provided with rather fine winged reticulations (1-3μ wide by 1μ deep), and 10-15μ, rarely 17μ, in length.

Hosts and Distr.: *Polygonum Convolvulus* (?), Mt. Carmel, May 8, 1904 (last year's flowers); *Polygonum dumetorum* var. *scandens,* Montowese, Sept. 14, 1903; New Canaan, Sept. 29, 1903.

This species is closely related to the next, but differs in having usually lighter colored and somewhat larger spores, with finer reticulations.

Ustilago utriculosa (Nees.) Tul. Figs. 4, 21, 54. The sori destroy the essential organs of all of the flowers, and form ovate, dusty, purplish spore masses 3-4 mm. in length, protected at first by the floral envelopes. The spores are violet or purplish, chiefly subspherical or spherical, provided with rather coarse, winged reticulations (2-4μ wide by about 1.5μ deep), and chiefly 9-14μ in diameter.

Hosts and Distr.: *Polygonum Hydropiper,* Montowese, Sept. 20, 1902; *Polygonum hydropiperoides,* Whitneyville, July 24, 1902; *Polygonum lapathifolium,* Westville, Sept. 2, 1902; *Polygonum Pennsylvanicum,* Westville, Sept. 2, 1902; Hamden, Sept. 11, 1902; Hartford, Oct. 20, 1902; Glastonbury, Oct. 23, 1902; Yalesville, Sept. 11, 1903, Oct. 14, 1904; Montowese, Sept. 14, 1903; New Canaan, Sept. 29, 1903; Manchester, Oct. 2, 1903; Green's Farms, Sept. 30, 1904.

This is one of the most common smuts of the state, especially on the last host.

Sphacelotheca DeBy.

The sori are usually found in the inflorescence (often confined to the ovaries), are provided with a false membrane of fungous cells that soon ruptures, disclosing a dusty spore mass and a central columella composed chiefly of plant tissues. The false membrane is formed largely or entirely of definite sterile fungous cells which are hyaline or slightly tinted, and vary in shape from linear to subspherical or cuboidal, and in size from less than to larger than the spores. The spores are like those of *Ustilago,* simple, free, usually reddish brown, and of small to medium size. Figs. 5, 6, 37, 38.

Very often groups of the sterile subspherical cells are scattered through the spore mass. The columella is usually the remains of the woody plant tissues, and often protrudes above

the spore mass as the latter wears away. See Fig. 37. This genus has not been thoroughly worked up for the whole world, and so a number of the species belonging under it are now included under *Ustilago*. Only two of the 16 species occurring in North America are of economic importance. So far only two species have been found in Connecticut.

Key to Species of Sphacelotheca.

I. Spores olive brown, smooth.....*S. Sorghi.*
II. Spores purplish, verruculose.....*S. Hydropiperis.*

Sphacelotheca Sorghi (Lk.) Clint. Figs. 5, 24, 26, 38. The sori occur in the ovaries, forming oblong or ovate bodies usually 3-8 mm. in length, or rarely fusing the aborted spikelets into longer forms. The brownish false membrane wears away from the apex, revealing the olive brown spore mass and finally the evident slender columella. The sterile cells of the membrane easily break up into groups, and are hyaline, oblong to subspherical, and chiefly 7-18μ in length. The olive brown spores are subspherical or spherical, smooth, often have pitted contents, and are 5.5-8.5μ in diameter.

Hosts and Distr.: *Sorghum vulgare* var. *sorghum,* New Haven, Sept. 30, 1903; *Sorghum vulgare* var. *technicum,* New Haven, Sept. 20, 1901 (Rorer), Sept. 11, 1903.

This species was found on both sorghum and broom-corn grown at the Experiment Station. So far as I can learn, neither of these plants is grown commercially in the state, so the smut is of no economic importance here, though further west it often does considerable injury to these plants.

Sphacelotheca Hydropiperis (Schum.) DeBy. Figs. 6, 37. The sori are found in the ovaries, forming oblong or ovate bodies 3-5 mm. in length; with the false membrane dehiscing at the apex, and revealing the purple-black spore mass and finally the slender columella. The sterile cells, besides forming the false membrane, constitute part of the columella; they easily separate, are hyaline or slightly violet tinted, chiefly subspherical, and 6-17μ in length. The spores are purplish, broadly oblong or ovate to (chiefly) subspherical, very minutely but abundantly verruculose and 10-17μ in length.

Hosts and Distr.: *Polygonum acre,* Green's Farms, Sept.

30, 1904; *Polygonum sagittatum,* Westville, Sept. 2, 1902, Sept. 14, 1903 (Britton), Oct. 4, 1904; Montowese, Sept. 20, 1902; Whitneyville, Sept. 21, 1902; Centreville, Sept. 27, 1902; New Canaan, Oct. 9, 1902 (Britton), Sept. 11, 1903; Yalesville, Sept. 11, 1903; Andover, Sept. 15, 1903; Cheshire, Oct. 25, 1903.

This is another of the common smuts of the state, especially on the arrow-leaf Polygonum, and is found in the fall. It is the only purple-spored species of the genus, of which it is the type, however. Fig. 37 shows the smut on *Polygonum acre,* several of the sori exposing the slender central columella.

Cintractia Cornu.

The sori occur on various parts of the host, but most commonly in the ovaries; at maturity they form a firmly agglutinated, or more rarely a dusty, spore mass, which usually is protected at first by a false membrane of sterile threads or indefinite cells. The single spores develop centripetally around a central axis, the outermost wearing off as they ripen; they are usually of medium to large size, and of a dark reddish black color, often opaque. Figs. 8, 27, 28.

The species of this genus occur on the Cyperaceæ, or occasionally on related families. So far 17 species have been described, 13 occurring in North America, and 4 in Connecticut. None of the species are of economic importance.

Key to Species of Cintractia.

I. Sori dusty at maturity, concealed by the glumes.
   A. Spores usually irregular polyhedral.....*C. Cyperi.*
   B. Spores usually ovoid to spherical (often with hyaline wings) .....*C. Montagnei.*

II. Sori firmly agglutinated at maturity.
   A. Subspherical, in ovaries.....*C. Caricis.*
   B. Oblong to linear, surrounding base of pedicles..... *C. Junci.*

Cintractia Cyperi Clint. The sori occur in the interior of the spikelets, infecting all of the head, and are hidden by the enveloping glumes until finally the dusty spore mass sheds

out on their exterior. The spores are reddish brown, oblong to polyhedral, chiefly irregular, smooth, but often showing darker lines on surface due to pressure of spore mass, and 12-18μ, or (most elongated) even 22μ, in length.

Host and Distr.: *Cyperus filiculmis,* North Haven, July 26, 1902; Montowese, Sept. 14, 1903.

This species was described originally from this state by the writer, having been found not uncommon on the sand plains near North Haven and Montowese. The affected plants look very much like those free from the smut, but can usually be detected by the darker aspect of the spikelets, which in this sedge are clustered into heads.

Cintractia Montagnei (Tul.) Magn. The sori occur hidden in the ovaries, forming inconspicuous, oblong to subspherical, usually dusty spore masses. The spores are brown or brownish black, often compressed laterally, and so appearing ovoid to subspherical or occasionally more irregular and angled, smooth but minutely pitted, and 12-19μ, chiefly 13-16μ, in length; they are very often provided with conspicuous, hyaline, wing-like bladders on either side.

Host and Distr.: *Rhynchospora alba,* Berlin, Sept. 3, 1902; Cheshire, Oct. 25, 1903.

This is another smut readily overlooked, because the inconspicuous sori are hidden by the floral bracts.

Cintractia Caricis (Pers.) Magn. Figs. 8, 27. The sori form subspherical bodies about 3-4 mm. in diameter in the ovaries; at first the sorus is protected by a white membrane of sterile fungous tissue, but this soon wears off, revealing the black, firmly agglutinated spore mass, the spores of which gradually ripen and wear off toward the interior. The spores are black-brown, subopaque, chiefly irregular polyhedral, or occasionally ovoid to subspherical, smooth or pitted to granular or even papillate, and 16-27μ, chiefly 18-22μ, in length.

Host and Distr.: *Carex Pennsylvanica,* Rainbow, June 6, 1903; East Hartford, June 1, 1904 (Weatherby).

This variable smut has been reported on a large number of *Carex* species in North America, but the above is the one upon which it commonly occurs. The illustration shows it in the ovaries at the base of the staminate spikelet of this host.

Cintractia Junci (Schw.) Trel. Fig. 28. The sori are linear, usually surrounding the pedicles or peduncles for half or more of their lower length, occasionally developing in the basal parts of the flowers; they form a black, rather firmly agglutinated spore mass. The spores are black-brown, subopaque, oblong to irregular polyhedral or subspherical, very minutely pitted, and 14-22μ in length.

Host and Distr.: *Juncus tenuis,* Westville, June, 1891 (Thaxter); Milford, June 26, 1894 (Sturgis), July 27, 1902; Whitneyville, June 20, 1902.

This was one of the first smuts reported from North America, having been described by Schweinitz from Carolina in 1834. The figure shows one of the peduncles smutted for half its length.

Schizonella Schröt.

The sori form black agglutinated spore masses in the leaves. The spores are united in pairs (formed by internal division of a mother cell), and often become laxly connected by their bulging contiguous surfaces, or even entirely separated; they are of reddish brown color and of small or medium size. Figs. 9, 35.

Only one species, with a variety, is known for this genus, but it has a wide distribution on various species of *Carex.* In North America it has been found chiefly on *Carex Pennsylvanica,* its host in this state.

Schizonella melanogramma (DC.) Schröt. Figs. 9, 35. The sori form black, agglutinated, linear, elevated striæ, 1 or 2 mm. long, or, by terminal fusion, of considerable length, chiefly on the upper sides of the leaves. The spores are dark reddish brown, often with the cells entirely or partially separated by the bulging out of their contiguous surfaces, chiefly ellipsoidal to hemispherical, or, when separated entirely, polyhedral or subspherical, and 8-12μ in length.

Host and Distr.: *Carex Pennsylvanica,* Westville, July 12, 1902; Whitneyville, May 4, 1903.

This is a species found chiefly in the spring; it probably has a much wider distribution than indicated here.

Sorosporium Rud.

The sori occur in various parts of the host, forming dusty dark colored spore masses like *Ustilago*. The medium-sized spore balls are composed of numerous spores, often so loosely held together that in time they separate entirely. The spores are like those of *Ustilago*, simple, olive to reddish brown, and of medium size. Figs. 7, 36.

When the spore balls become separated into the individual spores, it is difficult to distinguish the species from *Ustilago*. The number of species described by Saccardo is over 30, but some of these probably belong under other genera. For North America 9 species are now known, and 2 or 3 of these occur in Connecticut.

Key to Species of Sorosporium.

I. Sori in ovaries, 1-2 cm. in length; spores 8-12μ..... *S. Everhartii.*

II. Sori involving the entire infloresence usually.

A. Sorus 1-5 cm.; spores 12-19μ.....*S. Ellisii.*

B. Sorus usually 3-7 cm.; spores 9-13μ..... *S. Syntherismæ.*

Sorosporium Everhartii Ell. & Gall. The sori develop in the ovaries, forming linear bodies 1-2 cm. in length, and are covered with a prominent whitish false membrane that dehisces at the apex into several lobes, disclosing the black-brown, semi-agglutinated spore mass and the flattened columella of plant tissue. The spore balls are oblong to subspherical, composed of many firmly agglutinated spores, and vary from 55 to 125μ in length. The spores are reddish brown, or the interior ones often nearly hyaline, ovoid to subspherical or polyhedral, smooth (outermost rarely granular), and 8-12μ in length.

Host and Distr.: *Andropogon scoparius,* Westville, Oct. 22, 1903; [Southington, July 16, 1902; North Haven, July 26, 1902; Montowese, Sept. 20, 1902; New Haven, Oct. 18, 1903].

The first specimen mentioned above is typical of the species as described here. Those included in the brackets were origi-

nally considered by the writer as belonging under *S. Ellisii,* since their sori involve the entire inflorescence, instead of being limited to the ovaries. The spores, however, are smaller than those of the typical members of that species, and both the spores and spore balls are like *S. Everhartii,* so they may possibly be only vigorous specimens of this species, in which the sorus has involved the whole inflorescence.

Sorosporium Syntherismæ (Pk.) Farl. Figs. 7, 36. The elongated sori usually involve the entire inflorescence, 3-7 cm. in length, or more rarely are limited to the individual spikelets, when they are shorter; they are provided with a prominent false membrane which ruptures irregularly, disclosing the black-brown spore mass, within which are often shredded filaments of plant tissues. The sterile cells of the membrane are hyaline, oblong to cubical or subspherical, and tend to adhere in filaments when crushed apart. The spore balls, often evanescent when old, are irregular oblong to subspherical, and 40-100μ in length. The reddish brown spores are minutely verrucose (the inner often smooth and more lightly colored), subspherical, polyhedral or occasionally more elongated, chiefly 9-13μ in length.

Host and Distr.: *Cenchrus tribuloides,* Savin Rock, Aug. 30, 1902; Montowese, Sept. 20, 1902.

This species should also be looked for on *Panicum prolifcrum,* which is a common host for it elsewhere.

Tolyposporium Wor.

The sori are usually found in the ovaries, forming a granular spore mass at maturity. The spore balls are of medium size, dark colored, and composed of numerous permanently united spores. The spores are bound together by ridged folds or thickenings of their outer walls, and are of small to medium size. Figs. 10, 40.

The spore balls can be ruptured by pressure, when the outer darker colored covering often breaks apart as ridges or spine-like projections on the light colored or hyaline spores. So far 13 species have been described, though it is doubtful if all belong to this genus; 2 of these occur in North America,

and 1 in Connecticut. None of the species apparently are of economic importance.

Tolyposporium bullatum (Schröt) Schröt. Figs. 10, 40. The ovate sori are found in the ovaries, are about 3-5 mm. in length, and are covered by a smooth greenish plant membrane, which upon rupturing discloses the granular, black spore mass. The spore balls are opaque, black, oblong to spherical or polyhedral, contain numerous (over 100) firmly agglutinated spores, and are 50-160μ in length. The spores are light reddish brown, or the inner ones semi-hyaline, and are covered with a thin, tinted outer coat thrown more or less into ridges or folds that bind the spores together; they vary from ovoid to spherical or polyhedral, and are 7-12μ, rarely 14μ, in length.

Host and Distr.: *Panicum Crus-galli,* Woodmont (Setchell); Unionville, Aug. 26, 1902; New Haven, Sept. 11, 1903; New Canaan, Sept. 29, 1903.

Sometimes *Ustilago sphærogena* occurs in the ovaries of the same plant with this. It can easily be distinguished from this by its larger sori, which are covered by a *hispid* membrane. Figure 40 shows the uppermost ovary only infected by the fungus.

TILLETIACEÆ Schröt.

The sori form dusty erumpent spore masses, or are permanently embedded in the plant tissues, often without evident distortion of these. The germination is by means of a promycelium, which usually gives rise to a terminal cluster of elongated sporidia, which sometimes bear whorls of similar secondary sporidia; or the primary sporidia, with or without fusing in pairs, may give rise to infection threads, or in a nutrient medium to a mycelium bearing dissimilar secondary sporidia (aerial conidia). Fig. 22.

Tilletia Tul.

The sori occur in various parts of the host, usually in the ovaries, forming a dusty, dark spore mass. The spores are simple, separate, and originate singly in the ends of special mycelial threads that generally disappear rather completely

through gelatinization; they are of large size, 16-35μ. Figs. 11, 12, 39.

This is the type of the family, and is one of the larger genera. The sorus is quite like that of *Ustilago,* but the spores are usually considerably larger. Saccardo records 53 species; 15 have been found in North America, but only 2 in Connecticut. The important stinking smuts of wheat, which cause so much damage in the western wheat districts, belong in this genus; but, as wheat is little grown in this state, neither species has been reported here. The smooth-spored species, *Tilletia fœtens* (B. & C.) Trel., however, has been found, on microscopic examination, in ground cattle food offered for sale in the state, apparently made from smutted western wheat. The cattle did not relish this food.

Key to Species of Tilletia.

I. Spores reticulate.....*T. Anthoxanthi.*
II. Spores apparently verruculose.....*T. Maclagani.*

Tilletia Anthoxanthi Blytt. Figs. 12, 39. The sori are ovate, about 3 mm. in length, and usually occur in all of the ovaries of the spike; they are somewhat hidden by the enveloping glumes, and at first are covered by a thin plant membrane, which eventually ruptures, disclosing the dusty, reddish black spore mass. Hyaline cells, or immature spores, are mixed with the spores, and are smaller than those, and have thin to medium-thick walls. The mature spores are reddish brown, ovoid to spherical, reticulate (3-6μ wide and 1-3μ deep), and 24-30μ, occasionally even 34μ, in length.

Host and Distr.: *Anthoxanthum odoratum,* Whitneyville, July 6, 1902.

The sori are so inconspicuous in the ovaries that the infected spikes scarcely differ in appearance from the normal. See Fig. 39, in which the spike is magnified two diameters. This European species has been found in this country only at the above station.

Tilletia Maclagani (Berk.) Clint. Fig. 11. The sori are found in the ovaries, and rarely also in the anthers, and are inconspicuous, being concealed by the enveloping glumes; upon

the rupture of the enclosing plant membrane, a dusty, reddish brown spore mass is disclosed. The spores usually show various stages of development, vary from light to dark reddish brown, are subspherical or spherical, or occasionally elongated or irregular, have a thick wall (3-4μ) apparently closely covered with verruculations (really very minutely areolately pitted), and are 18-27μ in length.

Host and Distr.: *Panicum virgatum,* Conn. (Herb. Farlow); East Hartford, July 7, 1903 (Weatherby).

The wild grass which is host for this smut is often cut for hay in the state, but it is doubtful if the smut does enough damage to be of economic importance.

Neovossia Körn.

The sori occur in the ovaries, forming dusty spore masses protected at first by a membrane of plant tissue. The large spores are simple, separate, and produced singly in the swollen ends of the special fertile hyphæ, which permanently invest them and taper into conspicuous elongated hyaline appendages. Fig. 13.

This genus is closely related to *Tilletia,* but can be distinguished by the tail-like appendage to the membrane investing the spores. There are only two species now known that properly come under this genus.

Neovossia Iowensis Hume & Hods. Fig. 13. The sori are found in the ovaries, are ovoid, about 2-3 mm. in length, and show inconspicuously between the spreading glumes. Sterile cells, or immature spores, which are hyaline, thick-walled, and chiefly smaller than the spores, are found in the spore mass. The mature spores are reddish brown, subopaque, ovoid, ellipsoidal, or rarely subspherical, provided with a hyaline envelope tapering into an irregular tail once or twice their length. They have a minutely reticulately pitted cell wall, and are 19-28μ by 13-19μ in size.

Host and Distr.: *Phragmites communis,* Montowese, fall, 1901 (Evans); Oct. 18, 1902.

This rare species, which has been reported elsewhere only from Iowa, was first found in this state by Professor Evans of Yale.

Urocystis Rab.

The sori usually occur in the leaves or stems, where they often cause considerable distortion, or more rarely in the floral parts, and form dark colored, dusty spore masses. The spore balls are permanent, composed of an enveloping cortex of tinted sterile cells, enclosing one to several spores, and are of small to medium size. The spores are reddish brown, and of variable shape and size. Figs. 14, 15, 41, 42.

The sori of this genus look very much like those of *Ustilago*. Saccardo in his *Sylloge Fungorum* describes 34 species; 12 of these occur in North America, and 4 have been listed from this state. A few of the species are of some economic importance.

Key to Species of Urocystis.

I. Spore balls usually with 1 fertile cell, rarely with 2; sori forming extended outbreaks on leaves and bulbs ..... *U. Cepulæ.*

II. Spore balls usually with 1 or 2 fertile cells, rarely with 3 or 4.

A. Sori forming pustular or irregular swellings on leaves and stem..... *U. Anemones.*

B. Sori in striæ usually on under side of leaf sheath ..... *U. occulta.*

III. Spore balls usually with 3 to 5 fertile cells, rarely with more; sori oblong in base of flowers..... *U. Hypoxyis.*

Urocystis Cepulæ Frost. Figs. 14, 42. The sori occur in the leaves and bulbs as isolated pustules or often as more extended areas, and are at first covered by a thin plant membrane, but eventually rupture this, disclosing a black, dusty spore mass. The spore balls are ovoid to spherical, small, 17-25μ in length, and contain one or rarely two spores. The sterile cells are tinted, ovoid to spherical, small, 4-8μ, and rather completely cover the spores. The spores are reddish brown, ovoid to spherical, and chiefly 12-16μ in length.

Host and Distr.: *Allium Cepa,* Green's Farms, June,

1890 (Thaxter), Oct. 22, 1902, June 24, 1904; Bridgeport, Sept., 1902; New Haven, June 23, 1904.

This is one of the most injurious smuts in this state. It occurs early in the season on the young seedlings, many of which may be killed outright, thus thinning out the stand irregularly. It is also found throughout the season, eventually doing considerable damage to the bulbs. The smut often becomes established in the soil, which is then rendered unfit for raising onions from seed. Sets, however, transplanted in the infected soil, suffer little from this trouble. Soil once infected remains so for years, and for this reason there is considerable land in the onion districts of the state that cannot be used to advantage for this crop. Experiments with treating the infected soil, at time of planting the seed, with various fungicides, such as formalin, and sulphur mixed with lime, have given some favorable results in keeping down the smut. As yet, however, such treatment is little practiced by the growers.

Urocystis Anemones (Pers.) Wint. The sori develop in the leaf blades, petioles, and stems, forming conspicuous pustules of varying shape and size, and soon disclose dusty, black spore masses. The spore balls are irregular, contain 1-5, usually 1-2 spores, and are 22-35μ, rarely 45μ, in length. The sterile cells usually incompletely cover the spores, and sometimes become separated from them; they are smoky brown or yellowish tinted, ovoid to spherical, and about 8-14μ in length. The spores are reddish brown, irregular, oblong or ovoid to polyhedral or subspherical, smooth, and chiefly 12-17μ, rarely 20μ, in length.

Host and Distr.: *Anemone nemorosa,* Milford, May, 1891 (Thaxter).

This smut is found early in the spring, and no doubt has a wider distribution and other hosts in the family Ranunculaceæ than that reported here.

Urocystis occulta (Wallr.) Rab. Figs. 15, 41. The sori of this smut are usually confined to the leaves, especially the inner side of the leaf sheaths, but occasionally occur in the culm or inflorescence; they form linear striæ of considerable length, and often are so closely placed that they merge into a dusty, reddish black stratum. The spore balls are ob-

long to subspherical, contain 1 or 2, rarely 3 or 4, spores, and are 16-32μ in length. The sterile cells usually incompletely cover the spores, are hyaline or yellowish tinted, and subspherical to oblong. The spores are reddish brown, oblong to subspherical, often irregularly flattened, smooth, and 11-18μ in length.

Host and Distr.: *Secale cereale,* Milford, June, 1890 (Thaxter); Rainbow, June 6, 1903.

The smut possesses some economic importance, since it occurs on cultivated rye. However, it apparently rarely becomes so abundant in the rye fields of this state as to cause serious injury. So far the writer has been able to find only a single smutted plant, though a number of fields have been examined.

Urocystis Hypoxyis Thaxt. The sori occur in the inner and basal parts of the flowers, distorting and destroying them more or less, and often run down somewhat on the pedicles; the infected parts have an irregular oblong shape, and finally disclose the dusty, purple-black spore mass. The spore balls vary from ovoid to spherical, contain 1-8, chiefly 3-5, spores, and are 25-60μ in length. The sterile cells completely cover the spores, are reddish yellow, ovoid, and 9-14μ in length. The spores are reddish brown, polyhedral, subspherical, or occasionally ovoid to oblong, and usually 13-16μ in length.

Host and Distr.: *Hypoxys erecta,* Westville, July, 1889 (Thaxter), July 12, 1902.

This smut was originally described from the specimens found by Professor Thaxter of Harvard in West Rock Park, Westville. Since then it has been reported from Massachusetts and South America.

Entyloma DeBy.

The sori occur chiefly in the leaves, being permanently embedded in their tissues, and forming discolored but usually scarcely distorted areas. The spores are hyaline or yellowish tinted, rarely darker colored, simple, separate, or occasionally slightly adhering together in rows or irregular masses, and of medium size. Elongated conidia are often produced from the

mycelium, protruding in tufts through the stomates. Figs. 16-18, 30-34.

About 70 species have been described, of which 25 occur in North America. Of the latter, four occur on cultivated hosts, but are not of especial economic importance. So far 8 species have been reported in Connecticut.

Key to Species of Entyloma.

I. Spores dark tinted, reddish brown, often adhering together.
  A. Sori forming minute, black, oblong or linear striæ.
    1. Spores golden brown, 7-11μ.....*E. lineatum.*
    2. Spores darker brown, 8-14μ...*E. crastophilum.*

II. Spores hyaline or yellowish tinted; sori forming discolored spots.
  A. Spores not apiculate, often adhering somewhat.
    1. With hypophyllous conidia or sporidia.
      a. Sori yellowish or reddish brown, 1-2 mm. *E. Thalictri.*
      b. Sori whitish or yellowish, 1-10 mm..... *E. Lobeliæ.*
      c. Sori yellowish or reddish, often bordered, ½-6 mm.....*E. Physalidis.*
    2. Usually without conidia.
      a. Sori light yellowish, ½-2 mm...*E. Linariæ.*
      b. Sori yellowish or reddish brown, 2-5 mm... *E. polysporum.*
  B. Spores apiculate and pedicellate, never adhering; sori yellowish, later reddish brown.....*E. Nymphææ.*

Entyloma lineatum (Cke.) Davis. Figs. 16, 32. The sori occur in the leaves, leaf sheaths, or occasionally in the culm, and are small, ½-3 mm. in length, subcircular to (chiefly) linear, scattered or fusing somewhat, lead-colored or black, and rather permanently covered by the epidermis. The spores are light golden brown, firmly agglutinated, usually ovoid to subspherical or somewhat polyhedral, smooth, and 7-11μ in length.

Host and Distr.: *Zizania aquatica,* New Haven, 1892 (Setchell); Whitneyville, July 24, 1902; Montowese, Oct. 18, 1902; Westville, Aug. 21, 1903.

Entyloma crastophilum Sacc. This species is closely related to the preceding, but differs in its slightly smaller sori and somewhat darker colored spores which are 8-14μ in length.

Host and Distr.: *Holcus lanatus,* West Haven, July 23, 1903; *Undetermined grass,* West Haven, Aug. 12, 1903.

Both this and the preceding species differ from the ordinary *Entylomas* in their darker colored spores.

Entyloma Thalictri Schröt. The sori are found in the leaves, forming small, angular, yellowish or reddish spots about 1-2 mm. in diameter, or by confluence becoming more extended and indefinite. The spores are hyaline or yellowish, ovoid to subspherical or occasionally somewhat angled and more irregular, thin-walled to medium thick-walled, smooth, and 8-13μ in length. The conidia are apparently produced on the under surface of the sori.

Host and Distr.: *Thalictrum polygamum,* Montowese, Sept. 14, 1903.

This species is not very common, and has been reported on the above host only from this state.

Entyloma Lobeliæ Farl. Figs. 17, 31. The sori form conspicuous whitish or yellowish areas in the leaves, and are 1-10 mm. in diameter. The spores are hyaline or yellowish tinted, oblong to subspherical or somewhat angled, rather thick-walled, and 11-15μ in length. The conidia form a whitish growth on the under surface of the sori, and are fusiform, and 10-25μ by 2-3μ in size.

Host and Distr.: *Lobelia inflata,* Hamden, Sept. 11, 1902; Hartford, Oct. 20, 1902; Cheshire, Aug. 3, 1903; Yalesville, Oct. 14, 1904.

This is probably the most common *Entyloma* occurring in the New England states, but so far it has been found only on the above species of Lobelia.

Entyloma Physalidis (K. & C.) Wint. Fig. 34. The sori form at first yellowish, but later darker colored, roundish or angular spots from ½-6 mm. in diameter. The spores vary from slightly tinted to light or reddish yellow, are ovoid, spher-

ical or slightly angled, have a thickish wall, and are 10-16μ in length. The conidia may occur on either surface of the sorus as a whitish growth, and are linear, somewhat curved, and 30-55μ by 1-2μ in size.

Host and Distr.: *Physalis pubescens,* South Manchester (Thaxter); New Haven, Sept. 16, 1902, Sept. 30, 1903; *Physalis Virginiana,* Hamden, Oct. 14, 1903.

The cultivated strawberry tomato, *Physalis pubescens,* is sometimes rather seriously injured by this smut. The figure shows the sori on this host, the spots having a definite darker border.

Entyloma Linariæ Schröt. Fig. 30. The sori show as small, faint, yellowish spots on the under surface of the leaves, and are oval to circular in outline, and ½-2 mm. in diameter. The hyaline or yellowish spores are chiefly subspherical or spherical, smooth, have evident double wall, and are 11-15μ, in length. The conidia have not been observed.

Host and Distr.: *Linaria vulgaris,* Westville, Oct. 22, 1903.

This species has been reported on this host only twice in North America. The variety is more common.

Entyloma Linariæ var. **Veronicæ** Wint. The sori are somewhat more evident than in the typical form of the species, showing on both sides of the leaf. The spores also are deeper tinted and larger, 13-16μ, or rarely 19μ, in length.

Host and Distr.: *Veronica peregrina,* New Haven, May 16, 1904.

Entyloma polysporum (Pk.) Farl. The sori form subcircular or more irregular, yellowish or (later) dark brown spots, 2-5 mm., in the leaves; the surrounding tissue is often killed, thereby merging the sori. The spores are usually hyaline to yellowish, or more rarely even chestnut brown, ovoid to spherical or somewhat polyhedral, smooth, provided with evident thick double wall, and chiefly 12-17μ in length. Conidia, apparently, are lacking.

Host and Distr.: *Ambrosia artemisiæfolia,* Cheshire, Aug. 3, 1903.

The closely related species *Entyloma Compositarum* Farl., also on Compositæ as hosts, probably also occurs in this state, though not yet reported.

Entyloma Nymphææ (Cunn.) Setch. Figs. 18, 33. The sori occur in the leaves, forming yellowish, or with age reddish brown, variable, usually irregular areas most prominent on the under surface. The hyaline spores are ovoid to subspherical, usually distinctly apiculate, and with remains of hypha as an appendage at opposite end, smooth or, under an immersion lens, very minutely verruculose, 10-14μ in length. Conidia have not been found, but the spores germinate *in situ.*

Hosts and Distr.: *Nuphar advena,* New Haven (Setchell); *Nymphæa odorata,* Ledyard (Setchell); Westville, Sept. 2, 1902, Oct. 3, 1904.

The appendaged and apiculate spores easily distinguish this species from any other. Fig. 33 shows the sori on a portion of the leaf of *Nymphæa odorata.*

Doassansia Cornu.

The sori occur on various parts of the host, usually in the leaves, and are rather permanently embedded in the tissues. The spores are united into large, permanent spore balls; these consist of a distinct cortical layer of sterile cells, with the spores entirely filling the interior, or limited to one or two layers beneath the cortex, while the interior is filled with sterile cells or threads. The spores are hyaline or yellowish tinted, smooth, and of small to medium size. Figs. 19, 22, 29.

Our knowledge of this and the next genus is largely due to the investigations of Professor Setchell of the University of California, but at one time a resident of this state, where he collected part of the material with which he worked. The species occur chiefly on plants growing in moist situations, especially on the Alismaceæ. Of the 24 species described, 10 occur in North America, and 5 in Connecticut. They are of no economic importance.

Key to Species of Doassansia.

I. Spore balls with spores entirely filling their interior; sori forming lead-colored, slightly elevated pustules in leaves.....*D. opaca.*

II. Spore balls with a single layer of spores within which are sterile cells.

A. Sori in the slightly swollen ovaries.....*D. occulta.*
B. Sori forming discolored areas in leaves.....
D. Martianoffiana.
C. Sori forming conspicuous distortions usually in leaves .....*D. deformans.*

III. Spore balls with several irregular layers of spores, within which are hyphal threads; sori indefinite, hidden in leaf petioles.....*D. obscura.*

Doassansia opaca Setch. Figs. 19, 22, 29. The sori form in the leaves evident lead-colored pustules, about 2-5 mm., which show as slight elevations on both surfaces; they are more or less scattered, usually in yellowish or reddish brown widely discolored areas. The spore balls are closely compacted in a single layer, occupying most of the space between the epidermal layers of the leaf, and consist of a distinct cortex with a mass of fertile cells entirely filling the interior; they are oblong to subspherical or cuboidal, and 200-300μ in greatest length. The cortical cells are reddish brown, oblong or subcubical, prominent, about 14-27μ in length. The spores are rather loosely compacted, chiefly subspherical, 10-15μ in diameter.

Host and Distr.: *Sagittaria variabilis,* Norwich, Aug. 14, 1889 (Setchell); New Haven (Setchell); Whitneyville, Aug. 10, 1902; Montowese, Sept. 20, 1902; Westville, Sept. 8, 1904.

A portion of one of the spore balls is shown in cross section in Fig. 19.

Doassansia occulta (Hoffm.) Cornu. The sori occur in the ovaries, forming swollen, ovate bodies. The spore balls consist of a distinct cortex within which is a single layer of fertile cells surrounding a central mass of parenchymatous tissue; they are subspherical or more irregular, and 100-160μ in length. The cortical cells are polyhedral or more elongated tangentially, and 8-10μ in length. The spores adhere rather firmly, and are about 10-12μ in length.

Host and Distr.: *Potamogeton Pennsylvanicus,* Norwich, Aug. 26, 1889 (Setchell); Bridgeport (Morong).

Doassansia Martianoffiana (Thüm.) Schröt. In this species the sori occur in the leaves, forming unthickened, yel-

lowish or eventually reddish brown subcircular spots, which sometimes merge into indefinite areas. The spore balls are situated in the spongy parenchyma of the leaf, and consist of a distinct cortex surrounding a single layer of fertile cells within which is a central mass of sterile cells; they are chiefly subspherical or spherical, and 100-160μ in diameter. The cortical cells are brown and small. The spores are slightly yellowish tinted, chiefly polyhedral or slightly elongated radially, and 8-12μ in length.

Host and Distr.: *Potamogeton* sps., Norwich (Setchell); New Haven (Setchell); Simsbury (Setchell); Whitneyville, Aug. 18, Sept. 21, 1902; Westville, Sept. 8, 1904.

Doassansia deformans Setch. The sori occur in various parts of the host, usually in the leaves, where they form conspicuous distortions in the midribs and petioles. The spore balls occur in the intercellular spaces, and consist of a cortical layer surrounding a single layer of fertile cells within which is a central mass of sterile cells; they are chiefly subspherical, and vary from 100-140μ in diameter. The cortical cells are polyhedral, occasionally slightly elongated tangentially, small, about 4-6μ by 8-12μ. The spores are ovoid to polyhedral, rather firmly united, and chiefly 8-12μ, rarely 15μ, in length.

Host and Distr.: *Sagittaria variabilis,* Norwich, Aug. 17, 1889 (Setchell); New Haven (Setchell).

This species was originally described by Setchell from Connecticut material.

Doassansia obscura Setch. The sori are obscured, the spore balls being hidden in the interior of the basal parts of the petioles without especial discoloration or distortion. The spore balls are arranged in a single row in the air chambers of the host, and consist of a distinct cortex surrounding several irregular layers of spores and a central mass of indefinite fungal hyphæ; they are oblong to subspherical, and of very large size, 150-300μ in length. The conspicuous cortical cells are light brown, ovoid to obovate or subcordate, and 12-18μ by 8-12μ. The spores are chiefly subspherical and small, 8-12μ in diameter.

Host and Distr.: *Sagittaria variabilis,* Norwich, Sept. (Setchell).

Setchell described this species originally from Connecticut and Massachusetts. This is the only collection reported for this state; the fungus is so hidden in the host that it is not easily detected.

Tracya Syd.

The sori occur permanently embedded in the tissue of the leaves (fronds). The spore balls are destitute of a cortical layer, and consist of a single layer of spores enclosing a network of septate filaments. The spores are hyaline or yellowish, firmly united, and of small to medium size. Fig. 20.

This genus, first described by Setchell under the name *Cornuella,* contains a single species, which has been reported only from North America and on a single species of duckweed. It is closely related to *Doassansia,* but lacks the sterile cortex.

Tracya Lemnæ (Setch) Syd. Fig. 20. The sori occur in the languishing fronds, showing the spore balls under a hand lens as minute, clustered or scattered, opaque embedded bodies. The spore balls are situated in the spongy parenchyma above the lower epidermis, are subspherical and rather small, 50-100μ in diameter. The spores are yellowish, firmly compacted, cuboidal, polyhedral or often more elongated radially, and chiefly 10-12μ in length; they arise from the ends of the sterile network of brownish hyphæ that fill the interior.

Host and Distr.: *Spirodela polyrrhiza,* New Haven (Setchell); Whitneyville, Oct., 1902.

This is one of the most interesting species of the Ustilagineæ. So far it has been reported only from four states. As in *Doassansia,* sections of the infected tissue are necessary to make out the structure of the fungus. Fig. 20 shows merely a portion of the spore ball in cross section.

LIST OF HOSTS, ACCORDING TO FAMILIES.

MONOCOTYLS.

NAIADACEÆ.

Potamogeton Pennsylvanicus.
Doassansia occulta.

Potamogeton sps.
Doassansia Martianoffiana.

ALISMACEÆ.

Sagittaria variabilis.
Doassansia deformans.
Doassansia obscura.
Doassansia opaca.

GRAMINEÆ.

Agrostis alba var. **vulgaris.**
Ustilago striæformis.
Andropogon scoparius.
Sorosporium ? Ellisii.
Sorosporium Everhartii.
Anthoxanthum odoratum.
Tilletia Anthoxanthi.
Arrhenatherum avenaceum.
Ustilago perennans.
Avena sativa.
Ustilago Avenæ.
Ustilago levis.
Cenchrus tribuloides.
Sorosporium Syntherismæ.
Eragrostis major.
Ustilago spermophora.
Euchlæna luxurians.
Ustilago Zeæ.
Glyceria grandis.
Ustilago longissima.
Holcus lanatus.
Entyloma crastophilum.
Hordeum vulgare.
Ustilago Hordei.
Ustilago nuda.
Panicum Crus-galli.
Tolyposporium bullatum.
Ustilago Crus-galli.
Ustilago sphærogena.
Panicum sanguinale.
Ustilago Rabenhorstiana.
Panicum virgatum.
Tilletia Maclagani.
Phleum pratense.
Ustilago striæformis.
Phragmites communis.
Neovossia Iowensis.
Secale cereale.
Urocystis occulta.
Setaria glauca.
Ustilago Panici-glauci.
Setaria Italica.
Ustilago Crameri.
Sorghum vulgare and vars.
Sphacelotheca Sorghi.
Zea Mays.
Ustilago Zeæ.
Zizania aquatica.
Entyloma lineatum.

CYPERACEÆ.

Carex Pennsylvanica.
Cintractia Caricis.
Schizonella melanogramma.
Cyperus filiculmis.
Cintractia Cyperi.
Rhynchospora alba.
Cintractia Montagnei.

LEMNACEÆ.

Spirodela polyrrhiza.
Tracya Lemnæ.

ERIOCAULACEÆ.

Eriocaulon septangulare.
Ustilago Eriocauli.

JUNCACEÆ.

Juncus tenuis.
Cintractia Junci.

LILIACEÆ.

Allium Cepa.
Urocystis Cepulæ.

AMARYLLIDACEÆ.

Hypoxys erecta.
Urocystis Hypoxyis.

DICOTYLS.

POLYGONACEÆ.

Polygonum acre.
Sphacelotheca Hydropiperis.
Polygonum Convolvulus (?)
Ustilago anomala.
Polygonum dumetorum var. **scandens.**
Ustilago anomala.
Polygonum Hydropiper.
Ustilago utriculosa.
Polygonum hydropiperoides.
Ustilago utriculosa.
Polygonum lapathifolium.
Ustilago utriculosa.
Polygonum Pennsylvanicum.
Ustilago utriculosa.

Polygonum sagittatum.
Sphacelotheca Hydropiperis.
NYMPHÆACEÆ.
Nuphar advena.
Entyloma Nymphææ.
Nymphæa odorata.
Entyloma Nymphææ.
RANUNCULACEÆ.
Anemone nemorosa.
Urocystis Anemones.
Thalictrum polygamum.
Entyloma Thalictri.
OXALIDACEÆ.
Oxalis stricta.
Ustilago Oxalidis.
SOLANACEÆ.
Physalis pubescens.
Entyloma Physalidis.
Physalis Virginiana.
Entyloma Physalidis.
SCROPHULARIACEÆ.
Linaria vulgaris.
Entyloma Linariæ.
Veronica peregrina.
Entyloma Linariæ
var. *Veronicæ.*
CAMPANULACEÆ.
Lobelia inflata.
Entyloma Lobeliæ.
COMPOSITÆ.
Ambrosia artemisiæfolia.
Entyloma polysporum.

EXPLANATION OF FIGURES.

Figs 1-20. Spores of various smuts, part of which are shown in optical cross section. Magnified about 650 diameters except where otherwise stated.

Fig. 1. *Ustilago longissima* from *Glyceria grandis.*

Fig. 2. *Ustilago Zeæ* from *Zea Mays.*

Fig. 3. *Ustilago Oxalidis* from *Oxalis stricta.*

Fig. 4. *Ustilago utriculosa* from *Polygonum Pennsylvanicum.*

Fig. 5. *Sphacelotheca Sorghi* from *Sorghum vulgare; a,* sterile cells of false membrane.

Fig. 6. *Sphacelotheca Hydropiperis* from *Polygonum sagittatum; a,* sterile cells of false membrane.

Fig. 7 *Sorosporium Syntherismæ* from *Cenchrus tribuloides; a,* spore ball magnified only about 100 diameters.

Fig. 8. *Cintractia Caricis* from *Carex Pennsylvanica.*

Fig. 9. *Schizonella melanogramma* from *Carex Pennsylvanica.*

Fig. 10. *Tolyposporium bullatum* from *Panicum Crus-galli; a,* spore ball magnified only about 100 diameters.

Fig. 11. *Tilletia Maclagani* from *Panicum virgatum.*

Fig. 12. *Tilletia Anthoxanthi* from *Anthoxanthum odoratum; a,* sterile cell.

Fig. 13. *Neovossia Iowensis* from *Phragmites communis.*

Fig. 14. *Urocystis Cepulæ* from *Allium Cepa.*

Fig. 15. *Urocystis occulta* from *Secale cereale.*

Fig. 16. *Entyloma lineatum* from *Zizania aquatica.*

Fig. 17. *Entyloma Lobeliæ* from *Lobelia inflata.*

Fig. 18. *Entyloma Nymphææ* from *Nymphæa odorata.*

Fig. 19. *Doassansia opaca* from *Sagittaria variabilis.* This is a cross section of a spore ball merely showing one end; *a,* superficial cortex of sterile cells; *b,* spores filling the interior of ball.

Fig. 20. *Tracya Lemnæ* from *Spirodela polyrrhiza.* This is a cross section of a spore ball merely showing one end; *a,* superficial layer of spores; *b,* sterile hyphæ filling interior of ball.

Figs. 21-25. Germination of spores of smuts. Magnified about 650 diameters.

Fig. 21. Germination of spore of *Ustilago utriculosa* from *Polygonum Pennsylvanicum* in water; *a,* promycelium; *b,* sporidia.

Fig. 22. Germination of spore of *Doassansia opaca* from *Sagittaria variabilis* in water; *a,* promycelium; *b,* sporidia; *c,* secondary sporidia fallen off.

Fig. 23. Germination of spore of *Ustilago Avenæ* from *Avena sativa* in horse dung; *a,* promycelium; *b,* infection threads.

Fig. 24. Germination of a sporidium of *Ustilago Sorghi* into an infection thread.

Fig. 25. Small portion of a group of sporidia developed from promycelium of *Tolyposporium Eriocauli* in potato agar.

Fig. 26. Cross section of epicotyl of broom corn infected by *Ustilago Sorghi; a,* epidermal cells; *b,* parenchyma cells of cortex; *c,* woody cells of central cylinder, and *d,* mycelium of the fungus ramifying through the parenchyma cells of the cortex. Magnified about 125 times.

Figs. 27-55. Sori of various smuts, showing general appearance and parts of different hosts infected. Natural size except where otherwise indicated.

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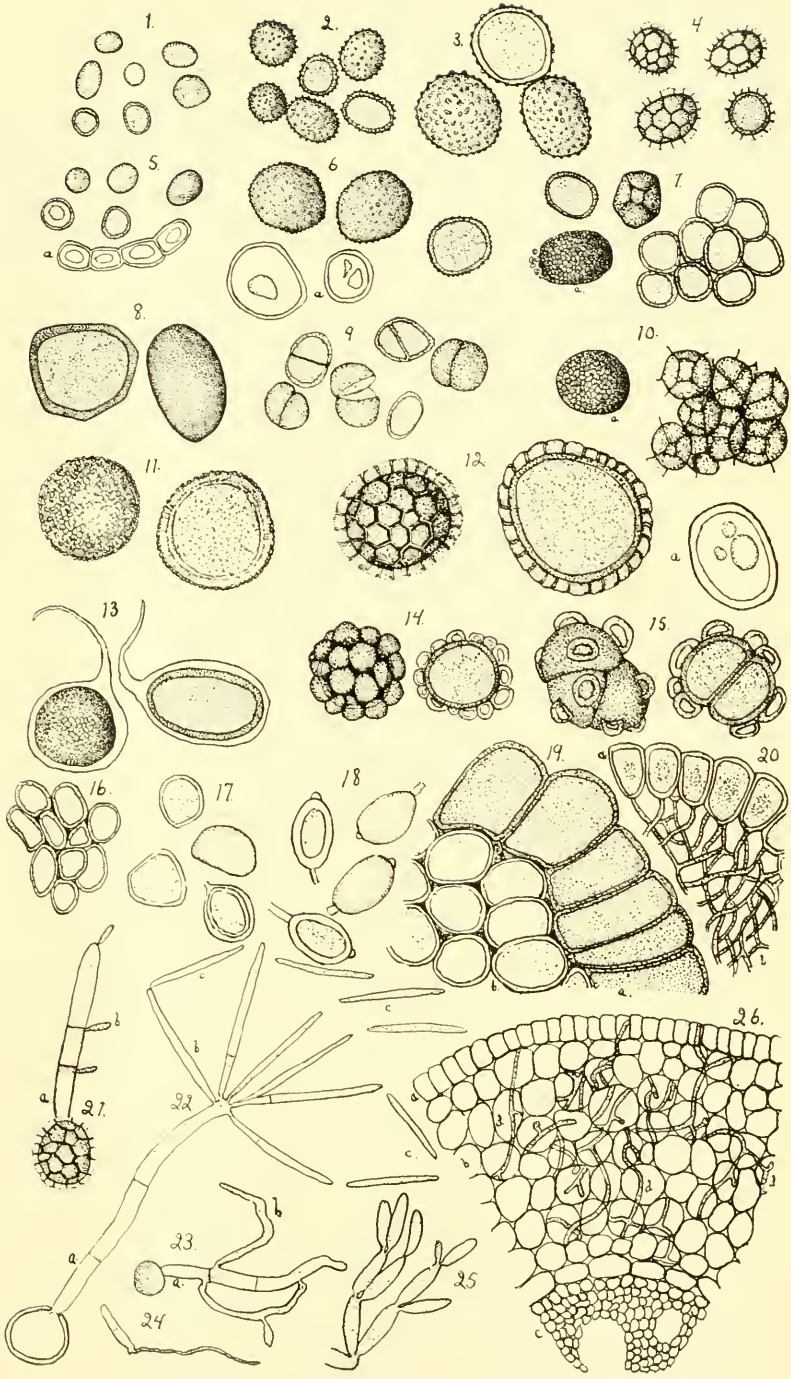
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Ustilago Crameri.

Fig. 45, p. 15.

Ustilago levis.

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Ustilago Hordei.

Ustilago nuda.

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Fig. 50, p. 17.

U. Rabenhorstiana

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U. striæformis.

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Ustilago spermophora

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U. sphærogena.

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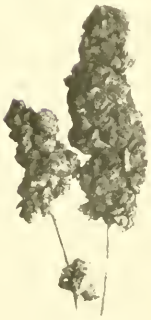

U. utriculosa.

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U. Zeæ ÷ ½.